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Description of four new species of limestone-associated *Torresitrachia* land snails (Mollusca: Pulmonata: Camaenidae) from the Katherine District of the Northern Territory, Australia, with comments on their conservation

RICHARD C. WILLAN[1], FRANK KÖHLER[2], VINCE KESSNER[3] AND MICHAEL F. BRABY[1,4]

[1]*Museum and Art Gallery Northern Territory, Department of Natural Resources, Environment, The Arts and Sport, GPO Box 4646, Darwin, NT 0801, AUSTRALIA*
[2]*Australian Museum, 6 College Street, Sydney, NSW 2010, AUSTRALIA*
[3]*162 Haynes Road, Adelaide River, NT 0846, AUSTRALIA*
[4]*Research School of Biology, Australian National University, Canberra, ACT 0200, AUSTRALIA*
Corresponding author: richard.willan@nt.gov.au

ABSTRACT

Four new species of land snails of the genus *Torresitrachia* (Pulmonata: Camaenidae) are described from the Northern Territory of Australia: *T. darwini, T. wallacei, T. cuttacutta, T. alenae*. The species are distinguished on the basis of differences in shell and animal morphology, and 16S DNA analysis. All four species occur in the Katherine District (Daly Basin Bioregion), and have remarkably small geographical ranges and fragmented populations. Though not all species of *Torresitrachia* are associates of limestone, these four species are obligately associated with limestone outcrops supporting monsoon/deciduous vine thicket vegetation. Annual grasses, which are replacing the natural vegetation, do not offer suitable habitat for these land snails and they are much more prone to the 'grass/fire cycle', thus threatening the snails' long term survival. Presently all the known populations of two of these new snails, *T. wallacei* and *T. alenae*, appear to be under threat of extinction and none occurs within any reserve.

Keywords: Mollusca, Pulmonata, Camaenidae, *Torresitrachia*, new species, Australia, Katherine, limestone outcrops, taxonomy, habitat fragmentation, conservation.

INTRODUCTION

Charles Darwin (1856) realised that land snails make excellent subjects for biogeographic analyses because of their limited powers of dispersal. His views were succinctly summarised by Örstan and Dillon (2009) who said: "Darwin's central thesis, that all organisms have diverged from common ancestors, required that they originate at single points, and disperse throughout the world. So if a convincing case could be built for land snails, surely to be ranked amongst the most disadvantaged of the world's dispersers, perhaps the remainder of the worldwide biota might fall into line."

Land snails do make good subjects for biogeographic studies, but unfortunately their populations are also very prone to fragmentation, leading to decline and often extinction of the species. Of all the major groups of invertebrates, the largest number of documented extinctions has occurred amongst the non-marine molluscs (Groombridge 1994). The extent of change to natural habitats right across the 'wet-dry' tropics of the north of the Australian continent has increased dramatically since European settlement almost certainly leading to substantial declines in abundance of endemic land snails. Already 31 species of land snails are listed as threatened by habitat loss in the Northern Territory, of which eight occur in the 'wet-dry' tropics (Woinarski *et al.* 2007). Thirty of these snails belong to the Camaenidae, but none of them is in the genus *Torresitrachia*.

Here we describe four new species of *Torresitrachia* occurring in the Katherine District (Daly Basin Bioregion as defined by Thackway and Cresswell (2005)) and restricted to limestone outcrops of the Tindall Limestone Formation where they have very small geographic ranges. Observations by one of us (Vince Kessner) spanning thirty years, plus our own quantitative surveys, have shown these habitats associated with the limestone outcrops are threatened by changed fire regimes with seasonal grasses replacing the closed monsoonal vine-thicket forest (*sensu* Wilson *et al.* 1990) with concomitant loss of leaf litter and increasing aridity of the soils (Braby *et al.* In prep.).

MATERIAL AND METHODS

The conchological separation of the four *Torresitrachia* species described here were made by comparisons between large numbers of specimens (numbers are given at the start of the Description for each species) jointly by Willan, Kessner and Köhler based on shell morphology and location. Köhler dissected two or three specimens of each species for the anatomical account and prepared the illustrations.

Table 1. List of sequenced samples of Camaenidae material (in addition to the four new species of *Toresitrachia* described herein) to construct the phylogenetic tree shown in Fig. 15.

Species	Material	GenBankAcc.	Location
Torresitrachia darwini sp. nov.	AM C.463000	GQ443623	NT, ca. 15 km NW of Katherine
Torresitrachia wallacei sp. nov.	AM C.462998	GQ443620	NT, 3.6 km NW of Katherine
Torresitrachia cuttacutta sp. nov.	AM C.462999	GQ443622	NT, 28 km S of Katherine
Torresitrachia alenae sp. nov.	AM C.462997	GQ443621	NT, 10 km NW of Katherine
Torresitrachia weaberana Solem, 1980	AM C.447629	GQ443625	WA, N of Kununurra
	AM C.460986	GQ443624	WA, NE of Kununurra, Weaber Ranges
Torresitrachia cf. *weaberana* Solem, 1980	AM C.462760	GQ443627	NT, Victoria River District
Torresitrachia cf. *bathurstensis* (E.A. Smith, 1984)	WAM S.37009	GQ443626	WA, Kimberley, Augustus Island
Setobaudinia anatispretia Solem, 1985	AM C.437624	GQ443619	NT, SE Timber Creek
Setobaudinia cf. *hirsuta* Solem, 1985	WAM S.36708	GQ443618	WA, Kimberley, South West Osborn Island
Setobaudinia cf. *interrex* Solem, 1985	WAM S.37031	GQ443617	WA, Kimberley, St. Andrews Island
Damochlora spina Solem, 1985	AM C.460993	GQ443616	WA, Mitchell Plateau
Amplirhagada castra Solem, 1981	AM C.460966	GQ443628	WA, Mitchell Plateau
Amplirhagada varia Solem, 1981	AM C.143841	GQ443629	WA, Mitchell Plateau

Köhler used one sample of each species to investigate genetic characters and assess relationships (Table 1). Braby undertook the spatial analysis and prepared the map (Fig. 14). All authors conferred on the conservation aspects, and the resulting text for these aspects was written by Braby and Willan using discipline-specific ecological terminology. Willan assembled the paper. Counts of shell whorls follow the description of Barker (1999).

Radulae and jaws were extracted manually, soaked in 10% potassium hydroxide solution, rinsed in fresh water, and mounted on carbon specimen tabs for scanning electron microscopy. The radular tooth formula shows the numbers of teeth as follows: C (central row of teeth) + number of lateral rows of teeth + number of transitional rows of teeth + number of marginal rows of teeth. Generally, we could observe only subtle differences in tooth and jaw morphology between the species and, given the small number of individuals we examined anatomically, we present our data here but have refrained from evaluating them. This is because the differences seem to be largely individual, while the overall tooth and jaw morphology is highly conservative.

The geographical distribution of land snails and extent of the Tindall Limestone Formation at Katherine was plotted on a spatial map using ArcGIS 9, ArcMap Version 9.2 software. The Geographic Information System (GIS) for geological layers of the Katherine region, supplied by the Northern Territory Geological Survey department, was derived from the Katherine 1:250,000 map sheet KA5309. Locations whose co-ordinates were not recorded at the time of collection, or are dubious, were excluded from both the lists of localities given under each species below and the databases used for generation of the map.

DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. A fragment of the mitochondrial 16S rRNA gene was amplified by PCR using the primers 16Scs1 (Chiba 1999) and 16Sbd1 (Sutcharit *et al.* 2007). Reactions were performed under standard conditions with an annealing step of 90s at 55° C. Sequences were aligned by use of Clustal X vs. 2.0 (Larkin *et al.* 2007) with default settings. The aligned sequence data were trimmed to a total length of 790 bp and comprised 16 sequences, including two *Amplirhagada* sequences that were used as the outgroup to root the tree. To reconstruct the phylogram we selected three additional species of *Torresitrachia*, three species of *Setobaudinia*, one species of *Damochlora* and two species of *Amplirhagada* for inclusion (Table 1). The species of *Setobaudinia* and *Damochlora* were selected because they are camaenids with flat shells reminiscent of those of *Torresitrachia*. A phylogenetic tree was reconstructed by application of the Maximum Likelihood algorithm (ML) using the software Treefinder (Jobb *et al.* 2004) with specifications for a general time reversible model of sequence evolution (GTR+I+Γ) as revealed by the hierachical likelihood test implemented in this analysis software.

Institutional abbreviations. AM – Australian Museum, Sydney; NTM – Museum and Art Gallery Northern Territory (formerly Northern Territory Museum, Darwin); VK – private collection of Vince Kessner, Adelaide River, Northern Territory; WAM – Western Australian Museum, Perth.

SYSTEMATICS

Torresitrachia Iredale, 1939

Torresitrachia Iredale, 1939. Gender feminine. Type species, by original designation, *Helix* (*Trachia*) *endeavourensis* Brazier, 1872 (= *Torresitrachia torresiana* Hombron and Jacquinot, 1841). Recent, Torres Strait, Queensland, Australia.

Nomenclatural remarks. According to B.J. Smith (1992: 162), the name *Torresitrachia* was first proposed by Iredale (1933), but that introduction constituted only a nomen nudum. It was validly described later by Iredale (1939) and subsequently revised by Solem (1979), who also described various new species from the Kimberley region of Western Australia and adjoining areas of the Northern Territory. Additional species were later added by Solem (1981) from the northern Kimberley and eastern Arnhem Land, and by Solem (1985) from the northern Kimberley. The type species, *Helix endeauvourensis* from the Endeauvour River, northern Queensland, has been treated as a junior synonym of *Torresitrachia torresiana* (Hombron and Jacquinot, 1841) from Ile Toud, Torres Strait, northern Queensland, by Iredale (1938). Whilst agreeing with Iredale with regard to this synonymy, Solem (1979) acknowledged that the relationships of the various nominal species group taxa described from the Torres Strait islands and subsequently synonymised with *T. torresiana* are in need of further scrutiny.

Diagnosis. Shell medium-sized with sunken to slightly elevated spire; umbilicus moderately open to nearly closed. Apical sculpture varying from rather smooth to pustulose or ridged. Teleoconch sculpture may comprise axial ribs or long spines. Shell surface supports pustulose microsculpture consisting of vertical, angled or spiral ridgelets, umbilical walls usually densely covered by setae. Aperture slightly to strongly deflected from axis of coiling, partly covering the umbilicus, with simple to slightly protruded basal lip and very thin parietal callus.

Penis with epiphallus and epiphallic caecum of variable size; inner wall of epiphallus with structures ranging from longitudinal ridges to complex pilasters; epiphallus separated from penial chamber by circular ridge or change in pilasters; inner wall of penial chamber with dense pustulation proximally and longitudinal pilasters distally. Vas deferens enters epiphallus through complex pilasters or pore. Penial sheath absent. Retractor muscle attached to mid-portion of epiphallus. Vagina and free oviduct of moderate length and width. Spermatheceal head expanded, reaching base of albumen gland. Hermaphroditic duct enters laterally on talon.

Distribution. Species of the genus *Torresitrachia* are found across the north of Australia, from Queensland to Western Australia, and also possibly New Guinea (Solem 1981).

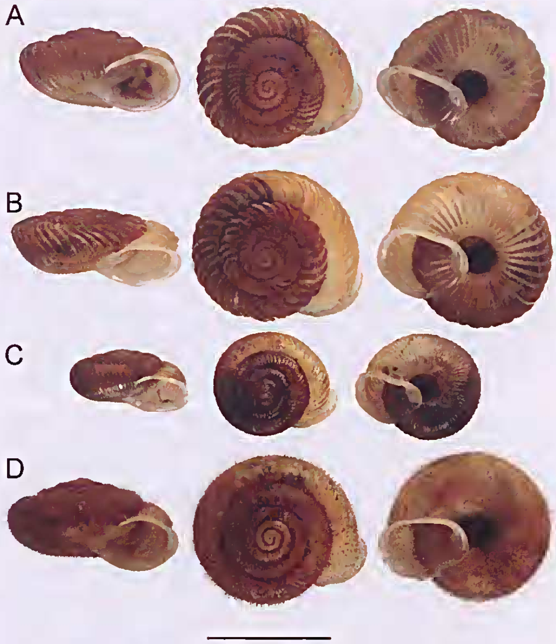

Fig. 1. Shells of holotypes of new *Torresitrachia* species shown in profile (left), dorsally (centre) and ventrally (right): **A**, *T. darwini* sp. nov. NTM P.43053; **B**, *T. wallacei* sp. nov. NTM P.43054; **C**, *T. cuttacutta* sp. nov. NTM P.43055; **D**, *T. alenae* sp. nov. NTM P.43056. Scale = 10 mm.

Torresitrachia darwini sp. nov.

Figs 1A, 2–4, 14

Material examined. Holotype – NTM P.43053 (ex AM C.463000), 13.2 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, ca. 15 km NW of Katherine, Katherine Rural College (14°23.683′S, 132°8.683′E), in deep leaf litter and under limestone slabs, intact and well-preserved vine thicket vegetation, large isolated limestone outcrop, coll. V. Kessner and M.F. Braby, 11 December 2008. Paratypes – AM C.463000, 32 specimens (of which 5 are cracked) in alcohol, same data as holotype; NTM P.42906, 12 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.42907, 12 dried shells, W Stuart Highway, 13.8 km NW of Katherine, Kintore Caves Reserve (14°24.438, 132°9.2′E), in deep leaf litter, intact and well-preserved vine thicket vegetation, large isolated limestone outcrop, V. Kessner and M.F. Braby, 11 December 2008; NTM P.42908, 8 dried shells, W of Stuart Highway, 3 km SSW of Katherine Rural College (14°23.933′S, 132°8.533′E), on soil surface under limestone rocks, limestone outcrop in open woodland with small patches of shady bushes, coll. V. Kessner, M.F. Braby and R.C. Willan, 25 January 2009; NTM P.42909, 20 dried shells, W of Stuart Highway, 2.6 km SSW of Katherine Rural College (14°23.7′S, 132°8.617′E), crawling on limestone rocks, on a large limestone outcrop with intact and well-developed vine thicket, during rain, at night, coll. V. Kessner and R.C. Willan, 25 January 2009; NTM P.43010, 25 dried shells, W of Stuart Highway, ca. 15 km NW of Katherine (14°23.683′S, 132°8.683′E), on surface of deep leaf litter, in a steep-sided limestone gorge, with intact and well-preserved vine thicket vegetation (tall grasses at mouth of gorge), part of a large isolated limestone outcrop, coll. V. Kessner, M.F. Braby and R.C. Willan, 25 January 2009; VK catalogue no. 12704, 28 dried shells, 3.5 km W of Stuart Highway, 10.2 km NW of Katherine (14°24.75′S, 132°10.333′E), coll. V. Kessner, 1 April 1988; VK catalogue

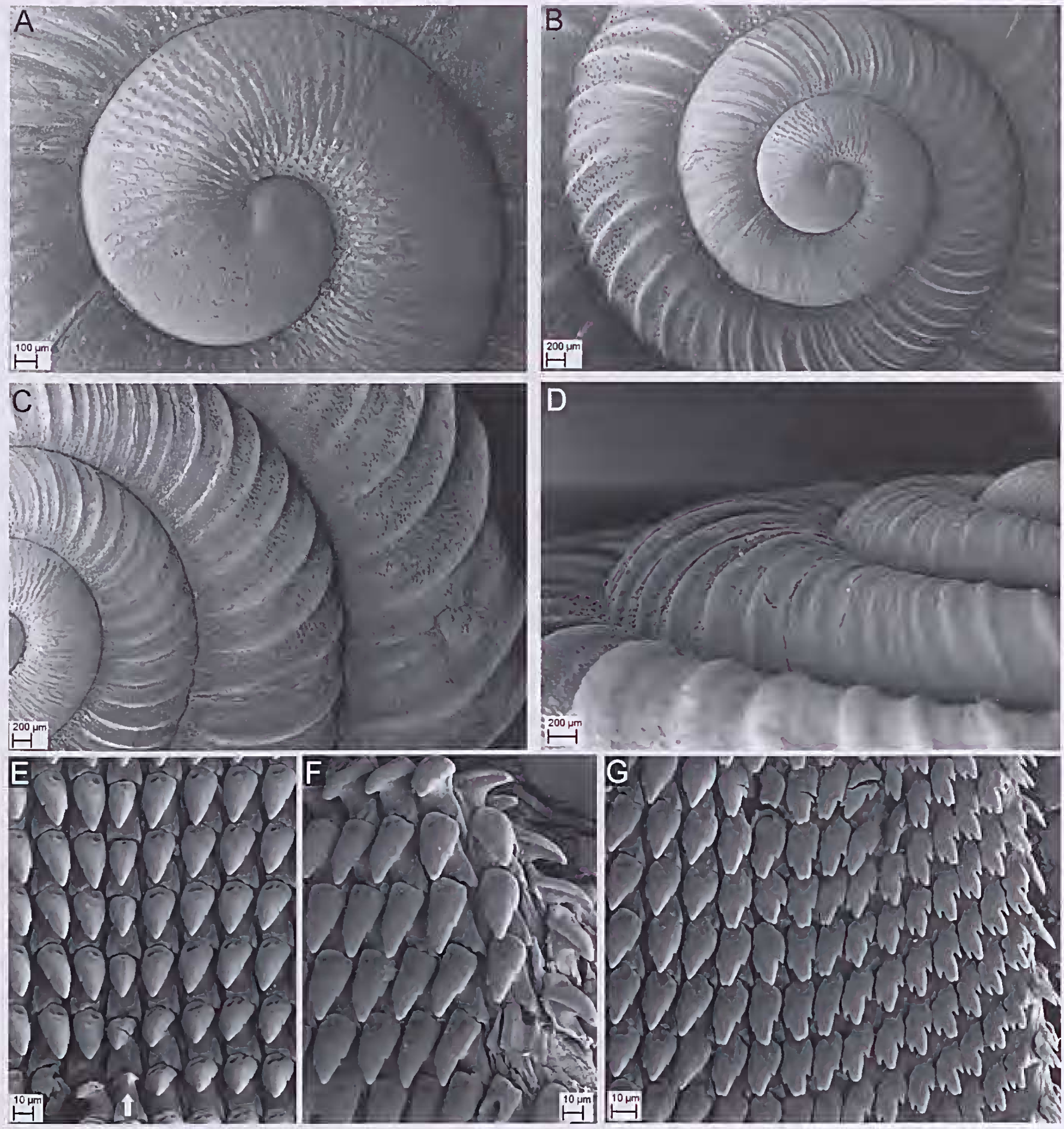

Fig. 2. SEM photographs of shells and radula of *Torresitrachia darwini* sp. nov., paratypes AM C.463000: **A,** Close-up of protoconch (scale 100 µm); **B,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **C,** Sculpture across all whorls of shell viewed from above (scale 200 µm); **D,** Lateral view of shell (scale 200 µm); **E,** Central (white arrow) and inner lateral teeth (scale 10 µm); **F,** Close-up of lateral teeth (scale 10 µm); **G,** Outer lateral and inner marginal teeth (scale 10 µm).

no. 12705, 40 dried shells, W of Stuart Highway, Katherine Rural College, 2.5 km SW of main campus (14°23.5´S, 132°8.5´E), coll. V. Kessner, 1 April 1988; VK catalogue no. 12706, 39 dried shells, W of Stuart Highway, Katherine Rural College, 3.6 km S of main campus (14°24.083´S, 132°8.167´E), coll. V. Kessner, 1 April 1988; VK catalogue no. 29284 NT-126/08, 17 dried shells, same data as holotype; VK catalogue no. 29285 NT-127/08, 17 dried shells, W. of Stuart Highway, 13.8 km NW of Katherine, Kintore Caves Reserve (14°24.438´S, 132°9.2´E), coll. V. Kessner and M.F. Braby, 11 December 2008; VK catalogue no. 29419 NT-005/09, 5 dried shells, W of Stuart Highway, 2.6 km SSW of Katherine Rural College (14°23.7´S, 132°8.617´E), coll. V. Kessner, M.F. Braby and R.C. Willan, 26 January 2009; VK catalogue no. 29420 NT-001/09, 25 dried shells, W of Stuart Highway, 3 km SSW of Katherine Rural College (14°23.933´S, 132°8.533´E), coll. V. Kessner, M.F. Braby and R.C. Willan, 26 January 2009.

Description. Based on 269 specimens.

Shell (Figs 1A, 2A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, with slight angulation at upper whorl, rounded above, rounded to slightly flattened below. Colour uniform, light brownish to horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 2A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch sculpture consisting of pronounced, distinct, regularly spaced axial ribs, curved if viewed from above, elongate and rounded in cross-section; interspaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell though less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Fine granulate periostreal sculpture visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, widely expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 3, 4). Penis coiled, much longer than free anterior part of oviduct; epiphallus moderately long, less than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long, shorter than epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal half of inner penial wall covered with well-developed, large, rhomboid pustules, densely arranged in honey-comb pattern, distal half with 4 to 5, well-developed, longitudinal, smooth pilasters; penial retractor muscle relatively long, still much shorter than penis, innervating more or less at anterior end of epiphallus. Vas deferens rather straight, thin, entering directly into

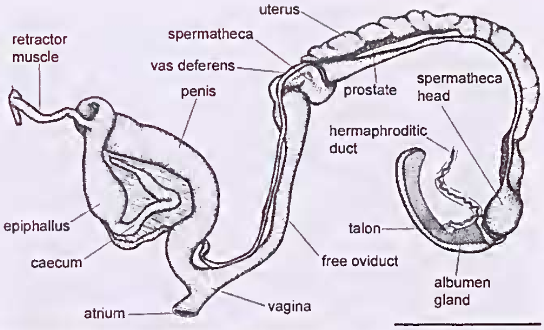

Fig. 3. Genital system of *Torresitrachia darwini* sp. nov. Scale 5 mm.

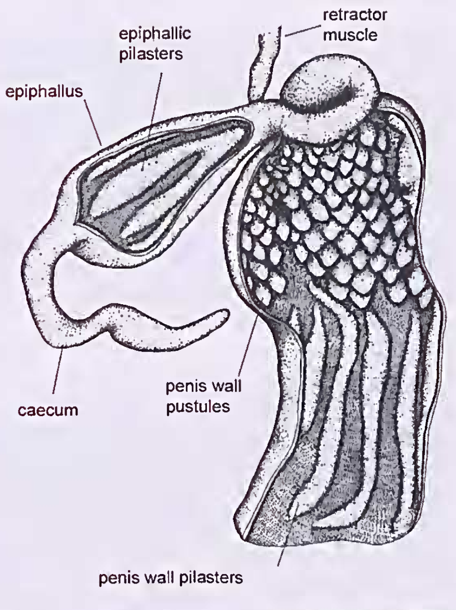

Fig. 4. Detail of penis of *Torresitrachia darwini* sp. nov. Penial wall opened proximally and distally to reveal detail of internal ornamentation. Scale 0.5 mm.

Table 2. Comparative shell measurements for the four species of *Torresitrachia*. Data given as range (mean ± standard deviation) in mm. n = number of specimens measured; **H** = shell height; **D** = maximum diameter of body whorl; **LW** = height of body whorl; **U** = maximum width of umbilicus; **W** = total number of whorls (teleoconch plus protoconch); **H/D** = ratio between height and maximum diameter of shell.

Species	n	H	D	LW	U	W	H/D
T. darwini sp. nov.	9	6.0 – 7.6 (6.9 ± 0.5)	11.8 – 13.5 (12.8 ± 0.6)	5.0 – 6.3 (5.9 ± 0.4)	2.5 – 3.5 (3.1 ± 0.3)	4.5 – 5.0 (4.6 ± 0.2)	0.50 – 0.60 (0.54 ± 0.03)
	Holotype (NTM P.43053)	7.1	13.2	6.3	3.0	4.5	0.54
T. wallacei sp. nov	14	6.4 – 7.3 (6.9 ± 0.3)	12.0 – 13.5 (12.9 ± 0.4)	5.6 – 6.2 (5.9 ± 0.2)	2.5 – 3.2 (3.0 ± 0.2)	4.5 – 4.9 (4.7 ± 0.1)	0.51 – 0.58 (0.53 ± 0.02)
	Holotype (NTM P.43054)	7.0	13.0	6.0	3.0	4.7	0.54
T. cuttacutta sp. nov.	7	4.3 – 5.3 (5.0 ± 0.3)	9.3 – 10.9 (10.0 ± 0.5)	4.1 – 4.6 (4.4 ± 0.2)	2.0 – 2.7 (2.4 ± 0.2)	3.0 – 3.6 (3.4 ± 0.2)	0.46 – 0.53 (0.50 ± 0.03)
	Holotype (NTM P.43055)	5.0	10.1	4.5	2.5	3.5	0.50
T. alenae sp. nov.	9	5.9 – 7.5 (6.6 ± 0.5)	12.5 – 14.0 (13.2 ± 0.5)	5.3 – 6.3 (5.8 ± 0.3)	2.5 – 3.5 (3.0 ± 0.3)	4.5 – 5.1 (4.7 ± 0.2)	0.46 – 0.54 (0.50 ± 0.03)
	Holotype (NTM P.43056)	7.5	14.0	6.3	2.9	4.9	0.54

epiphallus through pore. Vagina tubular, posteriorly inflated, rather long, interior with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct differentiated, duct moderately wide, inner wall with longitudinal pilasters, head narrowly elongated with markedly inflated tip, wall thin, inside densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus much longer than anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Figs 2E–G). Ribbon rectangularly elongate, on average 2.0 ± 0.0 mm long, with an average 72 ± 5 rows of teeth, 36.1 ± 2.6 rows/mm (n = 2). Tooth formula C + 9 –12 + 3–4 + 12–14. Central teeth with sharply pointed, elongate, triangular mesocones, of about as same length as base of tooth; central ectocoues tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of 2.6 km². One population occurs within the Kintore Caves Nature Reserve.

Comparative remarks. Among all the species described herein, *Torresitrachia darwini* sp. nov. has by far the shortest radula with the fewest number of rows. It is most similar to *T. wallacei* sp. nov. overall. Compared with this species however, the shell is larger (Table 2) and proportionately higher (larger H/D ratio, see Table 2), the angle between the axis of coiling and the aperture is considerably smaller and the last whorl is not as angulate. Compared with *T. alcnae* sp. nov., this species differs most conspicuously in shell sculpture (i.e., in possessing ribs rather than hairs). Shells of *T. cuttacutta* sp. nov. exhibit much denser and finer ribbing, the inner penial wall has finer, less regularly and densely arranged pustules, and the spermathecal head is not inflated.

Etymology. We name this species in honour of Charles Robert Darwin (1809–1882) on the 150th anniversary of publication of his seminal work *On the origin of species by means of natural selection*...(Darwin 1859). Darwin's interests lay in the biogeography and dispersal of freshwater and terrestrial molluscs and he undertook experiments with land snails to elucidate the mechanisms that may have brought them to oceanic islands (Örstan and Dillon 2009).

Torresitrachia wallacei sp. nov.

Figs 1B, 5–7, 14

Material examined. Holotype – NTM P.43054 (ex AM C.462998), 13.0 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, 3.6 km NW of Katherine (14°26.64′S, 132°14.28′E), under limestone slabs, open low limestone outcrops and sinkholes with scattered Rock Fig trees (*Ficus platypoda*) and by tall annual speargrass (*Sorghum macrospermum*), coll. V. Kessner, 25 January 2009. Paratpes – AM C.462998, 3 specimens in alcohol (of which 2 are cracked), same data as holotype; NTM P.42964, 8 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.7846, 6 dried shells, Kintore Reserve, N part of Kintore Caves system, in sediments, limestone cave outwash, coll. P. Bannink, 30 May 1993; NTM P.26178, 1 dried shell 12 km NE of Katherine, sorted from leaf debris, in mouth of a cave, coll. P. Bannink, 5 May 1994; NTM P.37748, 1 dried shell, Kintore Reserve, N part of Katherine Caves system, in leaf litter, at entrance to a cave, coll. P. Bannink, 4 September 1993; NTM P.37774, 3 dried shells, 10 km N of Katherine, N part of Katherine Caves system, in flood debris, on floor of a cave, coll. P. Bannink, 5 May 1994; NTM P.37778, 3 dried shells, 10 km N of Katherine, N part of Katherine Caves system, in flood debris, on floor of a cave, coll. P. Bannink, 21 May 1994; NTM P.42903, 8 dried shells, W of Stuart Highway, 3.7 km NW of Katherine (14°26.8′S, 132°14.28′E), under limestone slabs, low limestone outcrops and sinkholes with scattered Rock Fig trees (*Ficus platypoda*), coll. V. Kessner and M.F. Braby, 11 December 2008; NTM P.43070, 18 dried shells, limestone outcrop between Florina Road and Tokmakoff Road (14°28.433′S, 132°13.85′E) 'free sealer' under limestone rocks, in a low open limestone outcrop, coll. V. Kessner, 4 August 1986; VK catalogue no. 555, 12 dried shells, 1 km W of Stuart Highway, 3 km NW of Katherine (14°26.867′S, 132°14.05′E), coll. V. Kessner, 15 February 1980; VK catalogue no. 577, 4 dried shells, E of Stuart Highway, 4 km NW of Katherine (14°26.433′S, 132°14.267′E), coll. V. Kessner, 3 March 1979; VK catalogue no. 589, 7 dried shells, 0.5 km W of Stuart Highway, 3 km NW of Katherine (14°26.783′S, 132°14.767′E), coll. V. Kessner, 3 March 1979; VK catalogue no. 9417, 1 dried shell, E of Stuart Highway, 3 km NW of Katherine (14°26.533′S, 132°14.283′E), coll. V. Kessner, 4 August 1986; VK catalogue no. 9352 NM-010, 64 dried shells, limestone hillock near Springvale Homestead (14°29.963′S, 132°13.667′E), coll. V. Kessner, 20 May 1986; VK catalogue no. 9493, 27 dried shells, E of Stuart Highway, 3 km NW of Katherine (14°26.533′S, 132°14.283′E), coll. V. Kessner, 4 August 1986; VK catalogue no. 9494, 19 dried shells, limestone outcrop between Florina Road and Tokmakoff Road (14°28.433′S, 132°13.85′E) 'free sealer' under limestone rocks, in a low open limestone outcrop, coll. V. Kessner, 4 August 1986; VK catalogue no. 27325 NT-07/05, 9 dried shells, E of Stuart Highway, 3.3 km NW of Katherine (14°26.443′S, 132°14.133′E), coll. V. Kessner, 4 June 2005; VK catalogue no. 29286 NT-002/09, 7 dried shells, same data as holotype; VK catalogue no. 29293 NT-125/08, 4 dried shells, W of Stuart Highway, 3.6 km NW of

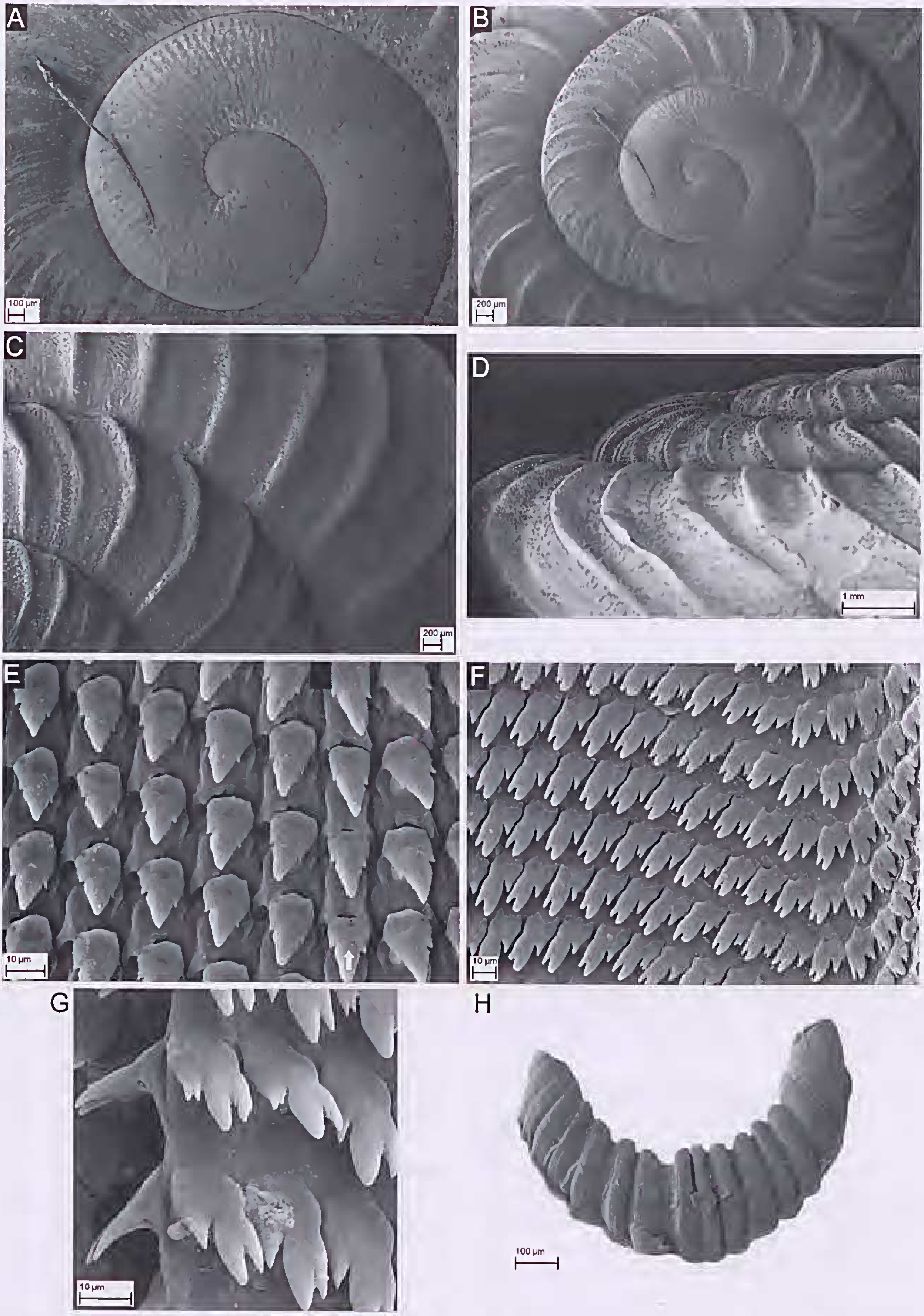

Figure 5. SEM photographs of shells, radula and jaws of *Torresitrachia wallacei* sp. nov., paratypes AM C.462998: **A,** Close-up of protoconch (scale 100 µm); **B,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **C,** Sculpture on second to fourth whorls viewed from above (scale 200 µm); **D,** Lateral view of shell (scale 1 mm); **E,** Close-up of central (white arrow) and inner lateral teeth (scale 10 µm); **F,** Inner and middle marginal teeth (scale 10 µm); **G,** Close-up of middle marginal teeth (scale 10 µm); **H,** Jaw (scale 100 µm).

Katherine (14°26.8´S, 132°14.283´E), coll. V. Kessner and M.F. Braby, 11 December 2008.

Description. Based on 174 specimens.

Shell (Figs 1B, 5A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, rounded to slightly angulate at upper whorl. Colour uniform, light brownish horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 5A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch sculpture consisting of strong, distinct, regularly spaced axial ribs, curved at shell angulation if viewed from above, elongately rounded in cross-section; interspaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell, less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Shell sparsely covered with fine granulate periostraeal sculpture, visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 6, 7). Penis coiled, longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long – about as long as epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal third of inner penial wall covered with well-developed, rather large, rhomboid pustules, arranged in honey-comb pattern, distal two-thirds with 4 to 5, longitudinal, smooth pilasters; penial retractor muscle very short, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, moderate in length, with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct slightly differentiated, duct

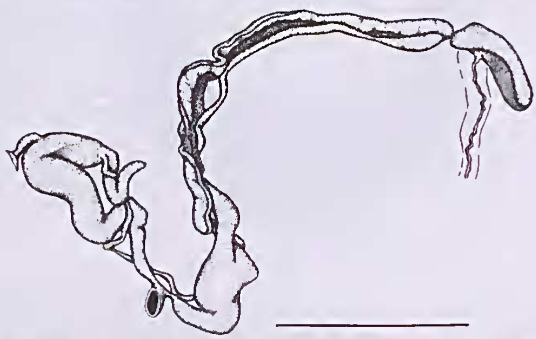

Fig. 6. Genital system of *Torresitrachia wallacei* sp. nov. Scale 5 mm. See Fig. 3 for labelling of organs.

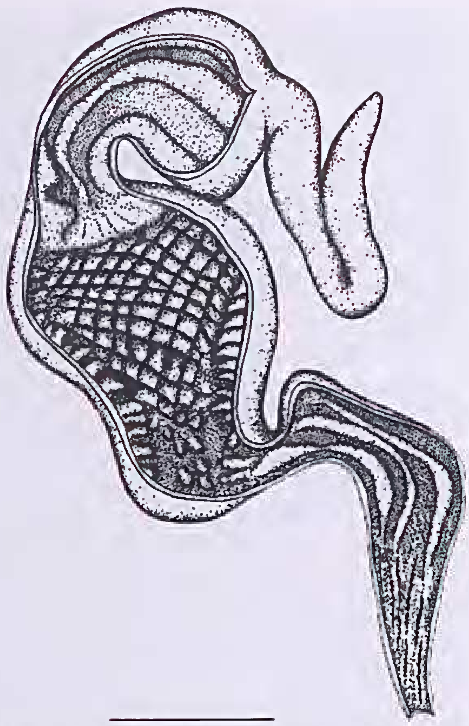

Fig. 7. Detail of penis of *Torresitrachia wallacei* sp. nov. Penial wall opened along its length to reveal detail of internal ornamentation. Scale 1 mm. See Fig. 4 for labelling of structures.

wide, inner wall with longitudinal pilasters, head narrowly elongate, tip slightly inflated with tubular to pyriform tip, wall thin, interior densely ciliated. Free oviduct rather short, coiled underneath entrance to uterus. Uterus of about same length as anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Figs 5E–G). Ribbon rectangularly elongate, on average 3.0 ± 0.5 mm long, with an average 126 ± 18 rows of teeth, 42.8 ± 0.9 rows/mm (n = 2). Tooth formula C + 10–12 + 3–4 + 10–12. Central teeth with sharply pointed, elongate, triangular mesocones, of about as same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones, split into 2 denticles.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of 4.9 km². No population occurs within any reserve.

Comparative remarks. The most distinctive feature of *Torresitrachia wallacei* is its depressed spire so that the upper surface of the shell is almost flat. Comparisons with the other species, particularly with *T. darwini* its closest relative, are given elsewhere in this paper.

Etymology. We name this species in honour of Alfred Russel Wallace (1823–1913) for independently proposing a theory of natural selection (Wallace 1870).

Torresitrachia cuttacutta sp. nov.

Figs 1C, 8–10, 14

Material examined. Holotype – NTM P.43055 (ex AM C.46299), 10.1 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, 28 km S of Katherine (14°32.167′S, 132°25.467′E), under limestone rocks, in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 26 January 2009. Paratypes – AM C.462999, 5 specimens in alcohol (of which 3 are cracked), same data as holotype; NTM P.42905, 20 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, S of Katherine). NTM P.37773, 9 dried shells, NTM P.37831, Cutta Cutta Caves (14°32.7′S, 132°25.8′E), in flood debris, on floor of a cave, coll. P. Bannink, 1 April 1994; NTM P.37836, 1 dried shell, Cutta Cutta Caves, Cutta Cutta Cave, in bark, 350 metres inside a cave, coll. A. Clarke, 1 April 1996; NTM P.37836, 1 dried shell, Cutta Cutta Caves, Water Resources Cave (14°32.7′S, 132°22′E), in deposits on floor of a cave, coll. A. Clarke, 2 April 1996; NTM P.9385, 7 dried shells, Cutta Cutta Caves, Tindal Cave (14°31′S, 132°25.8′E), in leaf litter, under a log, inside a cave, coll. S. Bone, 16 January 1997; VK catalogue no. 2168, 58 dried shells, W of Stuart Highway, 19 km S of Katherine (14°31.8′S, 132°25.617′E), coll. V. Kessner, 6 January 1979; VK catalogue no. 8222, 3 dried shells, Cutta Cutta Caves, 16 Miles Caves (14°34.7′S, 132°28.15′E), coll. V. Kessner, 19 June 1978; VK catalogue no. 9499, 30 dried shells, 19.3 km S of Katherine, W of Stuart Highway (14°32.233′S, 132°25.00′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9710, 90 dried shells, 19.3 km S of Katherine, W of Stuart Highway (14°32.233′S, 132°25.00′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9456 NW-002, 37 dried shells, 19.4 km S of Katherine W of Stuart Highway (14°31.417′S, 132°25.5′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9454 NW-009, 29 dried shells, 3 km W of Stuart Highway, Cutta Cutta Caves, Guy's Cave (14°34.983′S, 132°27.383′E), coll. V. Kessner, 19 May 1986; VK catalogue no. 12709, 4 dried shells, 24 km S of Katherine, 1.5 km W of Stuart Highway (14°33.617′S, 132°26.95′E), coll. V. Kessner, 1 April 1988; VK catalogue no. 3483, 11 dried shells, Tindal, Maud Creek Road, E of Katherine, N of Stuart Highway (14°28.7′S, 132°24.333′E), coll. P.A. Barden, 11 May 2007; VK catalogue no. 29288, 19 dried shells, same data as holotype.

Description. Based on 287 specimens.

Shell (Figs 1C, 8A–E). Relatively small (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl narrow to moderate, rounded with slight angulation at upper whorl. Colour uniform, light yellowish-brownish to horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 8A) rather smooth, sparsely covered with smooth, flattened pustules. Teleoconch sculpture consisting of narrow, distinct, regularly spaced axial ribs, slightly curved if viewed from above, squarish to rounded in cross-section; spaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell, less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Shell very sparsely covered with fine granulate periostracal sculpture, visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, widely expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 9, 10). Penis coiled, not much longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long, shorter than epiphallus, with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal third to half of inner penial wall covered with well-developed, rather small, rounded pustules, sparsely and irregularly arranged, distal two thirds to half with 4, rather thin, longitudinal, smooth pilasters; penial retractor muscle stubby, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, moderate in length, interior with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct differentiated, duct moderately wide, inner wall with longitudinal pilasters, head narrowly elongated with uninflated tip, wall thin, inside densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus about as long as anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Figs 8F–H). Ribbon rectangularly elongate, on average 2.3 mm long, with an average 101 rows of teeth, 44.7 rows/mm (n = 1). Tooth formula C + 9 –12 + 3–4 + 12–14. Central teeth with sharply pointed, elongate, triangular mesocones, of about same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring south of the Katherine River.

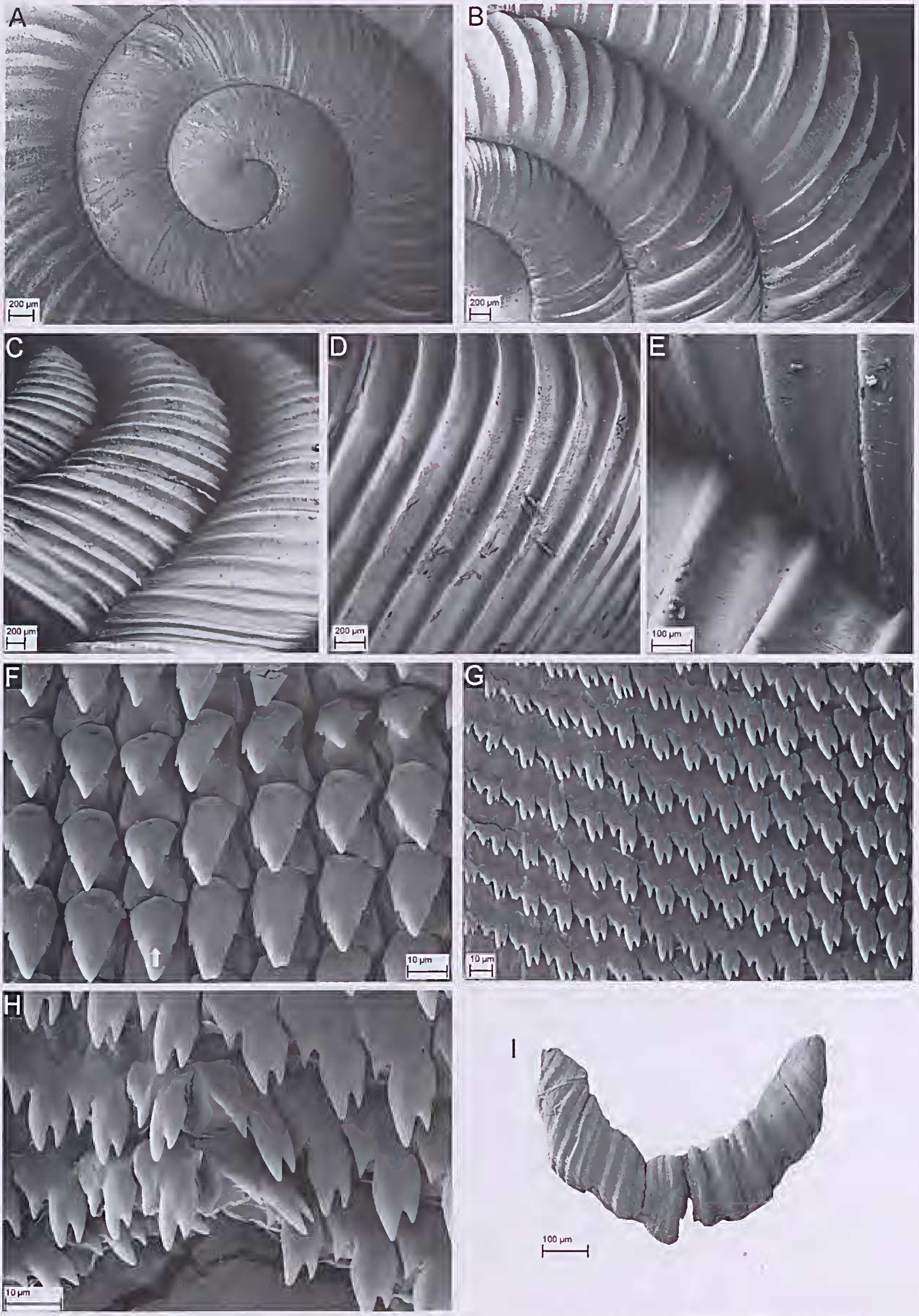

Figure 8. SEM photographs of shells, radula and jaws of *Torresitrachia cuttacutta* sp. nov., paratypes AM C.462999: **A,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **B,** Surface across all whorls of shell as viewed from above (scale 200 µm); **C,** Surface of third to fifth whorls viewed obliquely from above (scale 100 µm); **D,** Close-up of sculpture on body whorl (scale 200 µm); **E,** Details of sculpture at suture between body and penultimate whorl; **F,** Close-up of central (white arrow) and inner lateral teeth (scale 10 µm); **G,** inner and middle marginal teeth (scale 10 µm); **H,** Close-up of middle marginal teeth (scale 10 µm); **I,** Jaw (scale 100 µm).

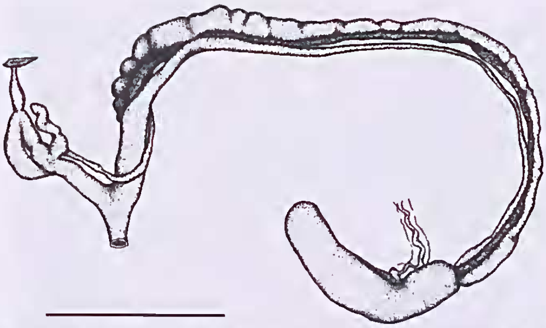

Fig. 9. Genital system of *Torresitrachia cuttacutta* sp. nov. Scale 2.5 mm. See Fig. 3 for labelling of organs.

Fig. 10. Detail of penis of *Torresitrachia cuttacutta* sp. nov. Penial wall opened distally to reveal detail of internal ornamentation. Scale 0.5 mm. See Fig. 4 for labelling of structures.

Present collections indicate an extent of occurrence of 20.4 km^2. One population occurs within the Cutta Cutta Caves Nature Reserve.

Comparative remarks. *Torresitrachia cuttacutta* sp. nov. is distinguished by its relatively small shell size (smaller when adult than any of the other three species). Compared to the three other species described herein it has finer axial ribs that are not as strongly elevated and are arranged more densely, the body whorl lacks angulation, and the lower part of body whorl is not as flattened. Furthermore, the pustulation of the inner penial wall is less developed, the pustules are not as densely packed, they are smaller and arranged randomly rather than in a honey-comb pattern, the penial pilasters are much smaller and thinner, and the uterus is much longer. The radular ribbon tends to be slightly shorter than in *T. wallacei* sp. nov. and it has fewer rows of teeth. Compared with *T. alenae* sp. nov., it differs most conspicuously in its shell sculpture (i.e., it possesses axial ribs instead of hairs).

Etymology. We name this species after its type locality, Cutta Cutta. It is intended as a noun in apposition.

Torresitrachia alenae sp. nov.

Figs. 1D, 11–13, 14

Material examined. Holotype – NTM P.43056 (ex AM C.462997), 14.0 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, E of Stuart Highway, 10 km NW of Katherine (14°24.367′S, 132°11.783′E), aestivating in leaf litter, under limestone rocks, in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 26 January 2009. Paratypes – AM C.462997, 21 specimens in alcohol (of which 5 are cracked), same data as holotype; NTM P.42904, 15 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.37736, 2 dried shells, 7 km N of Katherine, northern part of Katherine Caves system, in fig tree leaf litter on floor of a cave shaft, coll. P. Bannink, 7 May 1994; NTM P.37740, 1 dried shell, 7 km N of Katherine, northern part of Katherine Caves system, in leaf litter, cave flood debris, coll. P. Bannink, 7 May 1994; VK catalogue no. 29287, 24 dried shells, same data as holotype; VK catalogue no. 548, 26 dried shells, E of Stuart Highway, 10 km NW of Katherine (14°24.75′S, 132°12.5′E), in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 28 February 1979; VK catalogue no. 8602, 10 dried shells, E of Stuart Highway, 11 km NW of Katherine (14°24.167′S, 132°11.3′E), in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 20 March 1986.

Description. Based on 97 specimens.

Shell (Figs 1D, 11A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, angulate at upper whorl, rather flattened above and rounded below angulation. Colour uniform, light brownish horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 11A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch smooth except for faint axial growth lines; shell covered by hairs – density of hairs greatest on body whorl, quickly decreasing on penultimate whorl, and very sparse or absent on first whorl; hairs regularly distributed across whorl diameter, decreasing underneath suture, not present on umbilical sector of whorls where they are replaced by setae; no periostracal nodules on shell surface. Aperture wide; outer lip rounded

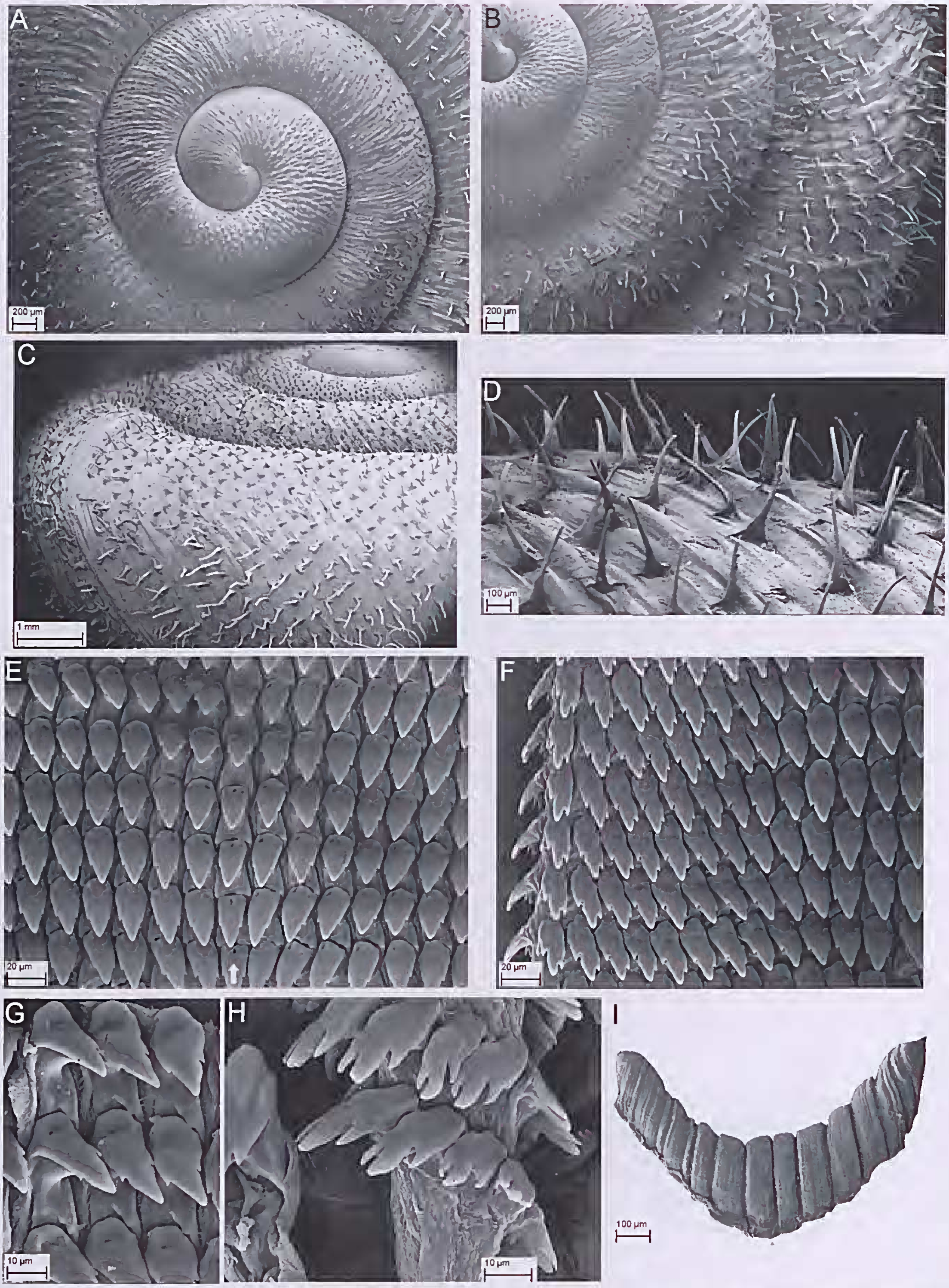

Fig. 11. SEM photographs of shells, radula and jaws of *Torresitrachia alenae* sp. nov., paratypes AM C.462997; **A,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **B,** Surface across all whorls of shell as viewed from above (scale 200 µm); **C,** Lateral view of body whorl (scale 1 mm); **D,** Close-up of hairs on body whorl (scale 100 µm); **E,** Central (white arrow) and lateral teeth (scale 10 µm); **F,** Outer lateral and inner marginal teeth (scale 20 µm); **G,** Close-up of inner lateral teeth (scale 10 µm); **H,** Close-up of middle marginal teeth (scale 10 µm); **I,** Jaw (scale 100 µm).

to slightly excavated, sharp, expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 12, 13). Penis coiled, much longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, very long, longer than epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal three-quarters of inner penis wall covered with well-developed, rhomboid pustules, arranged in honey-comb pattern, distal part with 4 longitudinal, smooth pilasters; penial retractor muscle very short, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, short, interior with broad longitudinal pilasters with transverse corrugations. Spermatheca long, reaching base of albumen gland; head and duct slightly differentiated, duct wide, inner wall with longitudinal, corrugated pilasters, head narrowly elongated, with inflated, club-like tip, wall thin, interior densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus of about same length as anterior part of oviduct or slightly longer. Albumen gland shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Fig. 8E–H). Ribbon rectangularly elongate, on average 2.7 ± 0.3 mm long, with an average 106 ± 10 rows of teeth, 39.1 ± 0.2 rows/mm (n = 2). Tooth formula C + 14 + 1–2 + 12. Central teeth with sharply pointed, elongate, triangular mesocones, of about same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones, split into 2 denticles.

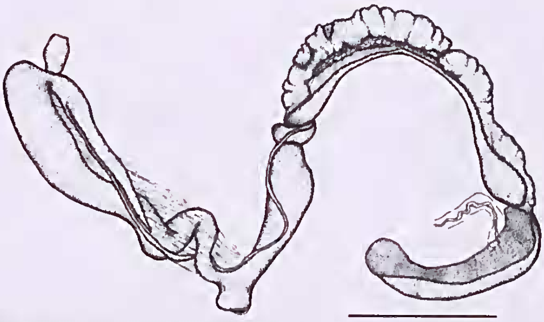

Fig. 12. Genital system of *Torresitrachia alenae* sp. nov. Scale 5 mm. See Fig. 3 for labelling of organs.

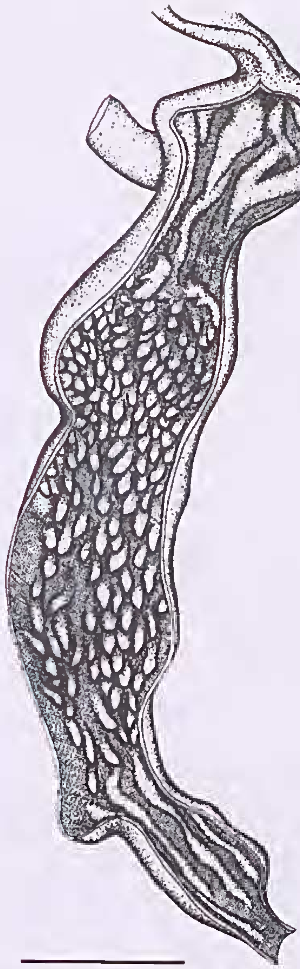

Fig. 13. Detail of penis of *Torresitrachia alenae* sp. nov. Penial wall opened along its length to reveal detail of internal ornamentation. Scale 1.5 mm. See Fig. 4 for labelling of structures.

Distribution. Endemic to the Tindall Limestone formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of only less than 1.0 km^2. No population occurs within any reserve.

Comparative remarks. *Torresitrachia alenae* is the only one of the four species described herein to lack axial sculpture and to have periostracal hairs on the shell surface. The pustulation on the inner penial wall is much longer than in any of the other species. The radular ribbon tends to be slightly shorter than in *T. wallacei* sp. nov., with fewer rows of teeth, and with slightly fewer rows of teeth per mm.

Etymology. We name this species in honour of Alena Kessner, wife of Vince Kessner, in recognition of her support through many years of Vince's molluscan obsession, both in the field and at home.

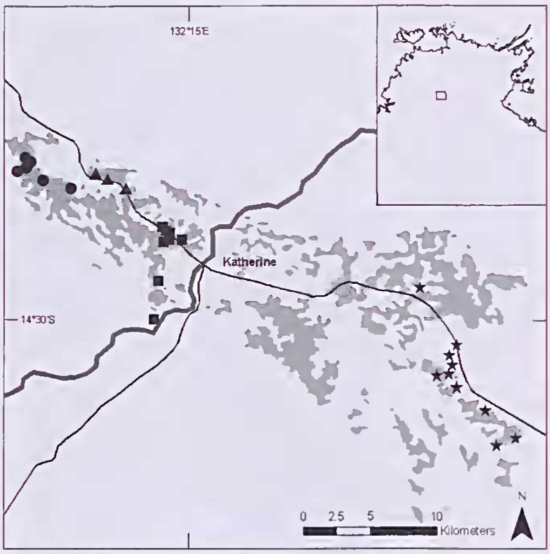

Fig. 14. Distribution map of *Torresitrachia* species: ● = *T. darwini* sp. nov.; ■ = *T. wallacei* sp. nov.; ★ = *T. cuttacutta* sp. nov.; ▲ = *T. alenae* sp. nov. Limestone outcrops are represented by shaded areas. The thick line represents the Katherine River and the thin lines represent major highways.

DISCUSSION

Three of the new species – *Torresitrachia darwini*, *T. wallacei* and *T. cuttacutta* – are morphologically (i.e., conchologically and anatomically) very close to each other. There are subtle and consistent differences between them, but as their populations are allopatric these differences could be due to intraspecific variation. However, their status as separate species is strongly supported by the degrees of genetic differentiation, with genetic distances between them ranging well above 10% (Fig. 15, Table 3). This is more than one would expect within the limits of a single species and together with the consistent differences in morphology, we can assume that there are probably four distinct species. *Torresitrachia darwini* and *T. wallacei* appear to be sister species, and *T. cuttacutta* is relatively close to them. Only *T. alenae* is clearly different by having hairs instead of axial ribs, and is only distantly related genetically.

The four species of *Torresitrachia* described here are united both geographically in their occurrence in the Katherine District and also ecologically in being apparently the only species of the genus obligately associated with limestone (calcium carbonate). According to our field observations, all are 'free sealers' in that they survive the long dry season in the litter or soil and seal the aperture with a calcified mucous covering (an epiphragm) that is porous yet offers protection from desiccation (Stanisic 2008).

Limestone outcrops in the 'wet-dry' tropics can be viewed as important refugia for the survival of land snails and the snails themselves are surrogates for measuring biodiversity conservation in the ecological communities in their specialised habitats (Stanisic 1999; Stanisic and Ponder 2004; Cameron *et al.* 2005; Slatyer *et al.* 2007). These limestone outcrops occur mainly in the drier inland areas of the monsoonal topics of northern Australia and their occurrence is sporadic. The outcrops frequently support pockets of dry rainforest (deciduous monsoon vine thickets) amidst a 'sea' of savannah woodland. Presumably the snails' dependence on limestone is related to the fact that calcium, which is readily available in these habitats, is required for shell growth and reproduction (Graveland *et al.* 1994). Thus these limestones afford the snails protection during the dry season when they are aestivating and an abundant source of calcium during the wet season when they are feeding and breeding.

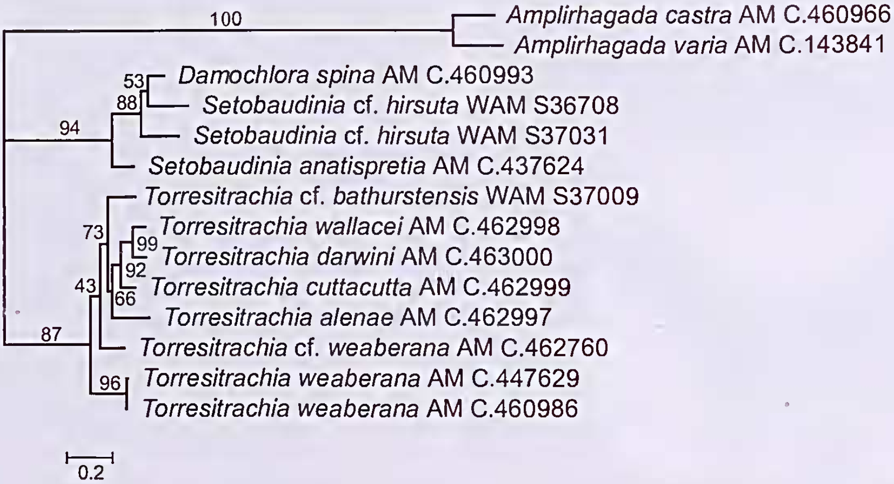

Fig. 15. Maximum Likelihood tree based on analysis of a partial fragment of the mitochondrial 16S rRNA gene (length of unaligned sequences approx. 750 bp) for a general time-reversible model of sequence evolution with gamma-distributed rate heterogeneity (GTR+I+Γ). Numbers on branches indicate nodal support by expected likelihood weights to all rearrangements of tree topology (WLW-LR; Strimmer and Rambaut 2002).

Table 3. Pair-wise genetic distances between the four *Torresitrachia* species. Corrected distances vary from 9.6% to 22.0%. Figure in upper rows = uncorrected p-distances; figure in lower row = corrected Tamura-Nei distances (Tamura and Nei 1993).

	T. alenae sp. nov.	*T. cuttacutta* sp. nov.	*T. darwini* sp. nov.
T. wallacei sp. nov.	0.165 0.220	0.101 0.121	0.082 0.096
T. alenae sp. nov.		0.149 0.194	0.158 0.207
T. cuttacutta sp. nov.			0.115 0.140

When the woodland surrounding these limestone outcrops is intact, densities of these land snails can be high (in the order of dozens per square metre), as at the type locality of *Torresitrachia darwini*. However, increased fire frequency, replacement of the existing forest by (native and introduced) annual grasses, reduction/elimination of the canopy, and high stocking rates of cattle during the wet season can reduce densities of these land snails dramatically (Woinarski *et al.* 2007) as at the type locality of *T. wallacei*. Fortunately there is no quarrying of the limestone for cement production as happens in other parts of Australia (e.g., Stanisic and Ponder 2004), South-East Asia (Clements *et al.* 2006) and many other parts of the world.

Fires pose the greatest threat to land snails (Stanisic and Ponder 2004), both generally and at the locations where these new taxa are found (Braby *et al.* In prep.). Fires affect snails directly by incineration and by dehydration, and indirectly through the destruction of their microhabitat (reduction of litter on the forest floor and soil moisture) (Stanisic and Ponder 2004; Stanisic 2008: 10). Fires now occur more frequently (probably annually close to the city of Katherine and near the Katherine River) than they did in the past. The grasses whose growth is promoted by fires increase the fuel load, which increases fire severity (frequency and/or intensity) and this leads to increased disturbance and decreased tree cover, which then facilitates further growth of grass. This cycle is known as the 'grass/fire cycle' (D'Antonio and Vitousek 1992). It may take many years for a fire-ravaged habitat to recover. Since the *Torresitrachia* snails in their limestone refugia are sensitive to desiccation, have poor tolerance to high temperatures and have no capacity to escape the fires (especially during the dry season when they are aestivating) (pers. obs.) they are going to be severely impacted by the 'grass/fire cycle' combined with habitat loss. Unless there is improved land management on the limestone outcrops in the Katherine district through fire suppression and control of grasses, some of the most localised of these limestone obligate *Torresitrachia* species, such as *T. wallacei* and *T. alenae*, may become extinct very soon (Braby *et al.* In prep.). They are certainly already seriously threatened.

Besides the snails of the genus *Torresitrachia* described herein, the miniscule pupillid snail *Gyliotrachela australis* (Odhner, 1917) is another limestone obligate restricted to the Katherine and Victoria River Districts. Other camaenids belonging to the genera *Xanthomelon* and *Setobaudinia* are endemic to the Katherine District, but are not restricted to limestones. They are not described yet, but are also already threatened by the same processes affecting the *Torresitrachia* species.

ACKNOWLEDGEMENTS

Peter Bannink, an ardent, Darwin-based speleologist, made collections of invertebrates from the caves he and his companions (Arthur Clarke and Sharon Bone) were exploring in the Katherine District in the 1990s and kindly donated them to the NTM. Peter's collections contain numerous land snails, including several species of *Torresitrachia*. The limestone outcrops where these new *Torresitrachia* snails occur contain fossil land snails and we are very grateful to Dirk Megirian for collecting some modern snails for the NTM mollusc collection during his palaeontological studies, including *T. wallacei*. We thank Brian Heim, Manager of Charles Darwin University's Katherine Campus, on which grounds the Katherine Rural College is located, for access to the limestone outcrops on that site. Philip Short of the Darwin Herbarium kindly identified the grass. Martin Püschel (AM) inked the drawings and photographed the shells, and Marlene Vial (AM) did the SEM work; the assistance of both of them is thankfully acknowledged. The authors thank John Stanisic and Winston Ponder for their comments on the manuscript for this paper. This project arose out of funding received from Natural Resource Management Board of the Northern Territory (Project number 2007083, to MFB) under the auspices of the Northern Territory Integrated Natural Resource Plan.

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